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The Kuleshov Effect: the influence of contextual framing on emotional attributions

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Filmmakers have long recognized the importance of editing techniques to guide the audiences' perceptions and enhance the impact of a scene. We demonstrate behaviorally that pairing identical faces with either neutral or emotionally salient contextual movies, an editing technique referred to as the 'Kuleshov Effect', results in both altered attributions of facial expression and mental-state. Using functional neuroimaging (fMRI), we show that faces paired with emotional movies enhance BOLD responses in the bilateral temporal pole, anterior cingulate cortices, amygdala and bilateral superior temporal sulcus relative to identical faces juxtaposed with neutral movies. An interaction was observed in the right amygdala when subtle happy and fear faces were juxtaposed with positive and negative movies, respectively. An interaction between happy faces and negative context was also observed in bilateral amygdala suggesting that the amygdala may act to prime or tag affective value to faces. A parametric modulation of BOLD signal by attribution ratings indicated a dissociation between ventrolateral and the ventromedial prefrontal cortex for negative and positive contextually evoked attributions, respectively. These prefrontal regions may act to guide appropriate choices across altering contexts. Together, these findings offer a neurobiological basis for contextual framing effects on social attributions.

Keywords: fMRI; kuleshov effect; context; affect; mental-state

Nearly a century ago, Soviet filmmaker Lev Kuleshov demonstrated that the manipulation of context can alter an audiences' perception of an actor's facial expressions, thoughts and feelings. For example, juxtaposition of identical archived clips of actor Ivan Mozzhukhin's face with either a scene of a funeral or a child playing led the audience to infer Mozzhukhin's emotional disposition as subtly melancholic or happy, respectively (Kawin, 1992). Despite the somewhat anecdotal nature of Kuleshov's observations, subsequent empirical work has confirmed that appropriate contextual framing will cause an observer to perceive neutral faces as happy or sad (Wallbott, 1988), angry faces as fearful (Carroll and Russell, 1996) and screams as joyful (Goldberg, 1951). Importantly, while this phenomenon is a ubiquitous tool of filmmakers it also speaks to the highly complex way in which context influences social attributions.

Contextual frames are presumably built up through real-world experiences whereby particular scenarios are experienced and subsequently influence how we perceive and predict the social world (Levanthal and Scherer, 1987;

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Bar, 2004). Social psychological studies have shown that when context is not taken into consideration, gross errors in attribution judgments can often be made (i.e. the correspondence bias) (Gilbert and Malone, 1995; Ross, 1977). The power of context has been demonstrated in studies of boundary extension and false memory experiments where contextually relevant information not present in, for example, a picture or story, is incorporated into subsequent judgments (Gottesman and Intraub, 1999; Loftus, 1997). Context also facilitates our ability to recognize stimuli otherwise imperceptible (Bar et al., 2006; Cox et al., 2004). According to theorists, context acts to alter our perceptions through expectations, presumably in a top-down manner (Bar, 2004). Contexts may also operate as nodes by which common events are organized in memory (Anderson and Bower, 1972; Bar and Aminoff, 2003). From an evolutionary standpoint, framing effects would improve fitness by optimizing predictions of imminent threat through, for example, constraining search within memory systems (Sahakyan and Kelley, 2002).

Neurophysiological studies of face perception in the primate brain have demonstrated a distributed network of interconnected regions, which contain face-selective cells (Rolls *et al.*, 2005). Most prominently, this network includes core face analysis regions in the fusiform gyrus (FFG) and superior temporal sulcus (STS), but also extends to higher-visual areas in the temporal pole and ventral prefrontal cortex (vPFC) (Haxby *et al.*, 2000; Rolls *et al.*, 2005; Tsao *et al.*, 2006). To date, the role of the extended face systems including the temporal pole and vPFC in face perception

remain speculative, particularly in humans. One theory is that these regions are involved in higher-order face perception, including social and contextual adjustments (cf. Haxby *et al.*, 2000). Although functional imaging studies have begun to demonstrate how context exerts powerful top—down control over the neural circuitry mediating memory and perceptual operations (Cox *et al.*, 2004; Maratos *et al.*, 2001; Bar *et al.*, 2006), little attention has been paid to how context influences socially relevant attributions.

We adapted the 'Kuleshov Effect' paradigm to elucidate the neural signature of contextual influences on face expression and mental-state attributions. While undergoing functional MRI, fourteen healthy volunteers were asked to rate emotional expression and mental-state (i.e. what the actor is thinking and feeling) from identical faces presented in negative, neutral and positively valanced contexts. As emotional context is enduring, and is not amenable to conventional event-related design, we used an epoch based event-related paradigm (Figure 1a) allowing us to statistically model phasic event-related activations. Since behavioral studies show that context is most effective when the clarity of the facial expression is low, but the clarity of the context is high (Ekman *et al.*, 1982; Trope, 1986), we used neutral faces and faces displaying subtly fearful and happy facial expressions (Figure 1b). To emphasize a link between the actors' faces and the contextual movie and reduce demand characteristics we chose to use a pseudo-candid photo manipulation, with subjects being led to believe that the actors' expressions were in response to viewing a juxtaposed movie (Figure 1c).

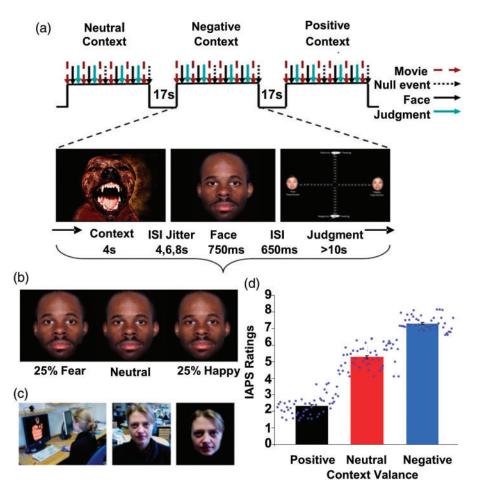


Fig. 1 (a) Schematic illustration of the paradigm. Participants were presented with 24 randomly allocated contextual epochs in a 3 × 3 factorial design with 8 negative, 8 positive and 8 neutral valance contexts counterbalanced across subjects. Each epoch began with a contextual movie presented for 4 s. A jittered interstimulus interval (ISI) followed, varying between 4 s, 6 s, and 8 s. Following this, a face with a neutral or subtle emotional facial expression was presented for 750 ms. After a short ISI of 650 ms, subjects were required to judge the face at a self-paced rate for emotional expression and mental-state using an orthogonal two-dimensional rating scale. Each epoch lasted up to 2 min, and involved six contextual movies, four or five juxtaposed faces and one or two null events. Each epoch was interleaved with a 17 s rest period. At the end of the scanning session subjects were again asked to rate each face but now with no context provided using the same orthogonal rating scale. (b) Example of neutral and computerized morphs of facial affect. (c) The pseudo-candid photograph manipulation: before each scan, subjects were told that the candid facial expressions were in response to seeing the juxtaposed movie. Subjects were first shown a picture of an actor viewing a movie and a webcam recording expressive facial responses to the movies. A representative picture of the actor's facial response to the movie was shown followed by an edited version on a black background. To protect against the possible confound of repetition effects, subjects were told that no face was shown more than once, although faces look similar due to the subtly of the expressions. To make this plausible, subjects were later converted into short movies.

METHODS

Participants

We scanned 17 healthy volunteers. Three subjects were later excluded due to a history of neurological problems (i.e. pediatric meningitis) and missing behavioral data. Post-scan questioning also revealed that one of the subjects 'guessed' the premise of the paradigm. The remaining 14 subjects (8 females: mean age and s.d. 27.5 ± 8.6) were all naïve to the premise of the study, English speaking, right-handed (Oldfield, 1971), had normal or correct vision and screened for history of psychiatric or neurological problems. All subjects gave informed consent and the study was approved by the joint Ethics committee of the National Hospital for Neurology and Neurosurgery (UCLH NHS Trust) and Institute of Neurology.

Experimental stimuli

We used 130 images taken from the international affective picture system (IAPS) (Lang et al., 1999). In addition, 14 supplementary images rated for valance by 10 volunteers were introduced to balance for content (e.g. humans, animals, objects, etc.) and visual complexity. Using the self-assessment manikin rating scale (Lang et al., 1999), three of the images were rated as positive (mean and s.d. 2.7 ± 0.5) and 11 were rated as neutral (4.9 ± 0.8) . Based on standard scores (1 = high)positive/9 = high their negative)(Lang, et al., 1999), and together with our additional set of images, 48 of the images were rated as positive (2.7 ± 0.6) , 48 as neutral (4.7 ± 0.9) and 48 as negative valance (7.7 ± 0.9) . Modeled on Kuleshov's original stimuli, our images were given a dynamic 'movie' effect by zooming in or out of the image. The use of dynamic, rather than static images provides a more vivid context (Wallbott, 1988). Both positive and negative contextual movies were significantly different for valance and arousal from the neutral movies (P < 0.0001).

The face stimuli were neutral, happy and fearful faces derived from the standardized NIM-STIM set. Thirty-six faces were presented in each context with 12 null events. An equal number of male and females faces balanced for ethnicity were used. Based on their standardized ratings, all faces were rated as significantly different for valence $(F_{2,22} = 23.9: P < 0.0005)$. To facilitate the influence of context (Ekman et al., 1982), we used FantaMorph 2.5 (http://www.fantamorph.com) to generate morphs between neutral and happy or neutral and fearful facial expressions. This process created two subtle facial emotions (i.e. 25% happy and 25% fearful). Post-hoc ratings of subtle face affect by the subjects showed significant differences between facial expression ratings $(F_{1.3,17.4} = 20.8: P < 0.0005;$ Greenhouse–Geisser corrected for non-sphericity; Figure 2a).

Experimental paradigm

Before each scan, the subject was told that the candid facial expressions depicted were captured in response to seeing the associated emotional or non-emotional movie. To facilitate this framing, we showed a pseudo-candid photograph illustrating the process in which face images were acquired (Figure 1c). Demand characteristics were reduced by telling the subjects that the study was concerned with the evaluation of everyday facial emotions in response to emotional material. In addition, subjects were told that all faces were different (i.e. no face was presented more than once), although this was not overtly evident due to the subtlety of the 'real' everyday emotions. Confounds such as familiarity or repetition effects were minimized by counterbalancing the stimuli across subjects. Subjects were given a practice session and told to rate each face for expression and mental-state (i.e. whether the actor is thinking positive or negative thoughts), emphasizing that the task was not to rate the movies.

Twenty-four randomly allocated epochs (contexts) were presented in a 3×3 factorial design with eight negative, eight positive, and eight neutral contexts, each lasting up to 18 min. Before each epoch began, a 17 s rest period was presented. Each epoch began with a contextual movie for 4 s. A jittered interstimulus interval (ISI) followed varying between 4 s, 6 s and 8 s. Following this, a face with a neutral or subtle facial expression was presented for 750 ms. After a short ISI of 650 ms, subjects were required to use a keypad to rate the face (at a self-paced rate, but timing out after 10 s) for emotional expression and mental state using an orthogonal two-dimensional rating scale based on Russell's Circumplex Model where values are recorded in Cartesian space (Russell, 1980). Each epoch lasted up to 2 min showing six contextual movies, and six events with up to five faces and no more than two null events. Following the scan session, each subject was asked to rate each face out of context (i.e. without the juxtaposed movie) for emotional intensity and mental state, again using the orthogonal rating scale. Stimuli were programmed using Cogent 1.24 (www.vislab.ac.uk).

fMRI acquisition

A Sonata 1.5T scanner (Siemans, Erlangen, Germany) was used to obtain gradient-echo, T2*-weighted echo-planar images (EPI) using a customized sequence to reduce signal dropout in the orbital frontal cortex (OFC) and amygdalar (Deichmann *et al.*, 2005). To prevent head motion, a head brace attached to the head-coil was used. We acquired 24 volumes (2 mm thick, 1 mm slice gap, providing approx 65% brain coverage) and tilted at -25° to capture several a priori regions of interest [i.e. FFG, OFC, anterior cingulate cortex (ACC), temporal pole, insula, STS, ventrolateral and ventromedial prefrontal cortex and amygdala]. This constrained approach was used for

two main reasons: (i) to maximize the temporal resolution and because (ii) we had no a priori reason to acquire parietal and superior occipital regions. Imaging parameters were as follows: repetition time (TR) = 2.16 s; echo time (TE) = 50 m; z shim prepulse = -1 mT/m* ms 3.0 mm; refocusing correction +5%; flip angle 84°; field of view (FOV) = 192×192 mm. We collected an average of 1347.1 ± 62.9 volumes per subject across three counterbalanced runs, including 15 dummy volumes (five in each run) to permit T1 equilibration (later discarded from the analysis).

Statistical analysis

parametric mapping (SPM2; Wellcome Department of Imaging Neuroscience, www.fil.ion.ucl.ac. uk/spm) was used to preprocess all fMRI data and included spatial realignment, slicetime correction, normalization and smoothing. To control for motion, all functional volumes were realigned to the mean volume, spatially normalized (Ashburner and Friston, 1999) to standard space Montreal Neurological Institute (MNI) template (Mazziotta et al., 1995) with a resample voxel size of $3 \times 3 \times 3$ mm and smoothed using a Gaussian kernal with an isotropic full width at half maximum of 10 mm. In addition, high-pass temporal filtering with a cut-off of 128s was applied to remove low-frequency drifts in signal and global changes were removed by proportional scaling. Following preprocessing, statistical analysis was conducted using the general linear model.

Analysis was performed to determine each subject's voxelwise activation during emotional events compared with neutral events. State-related neural activity was modeled with boxcar functions representing activity sustained throughout contextual epochs. This model was one of the regressors within the general linear model used to decompose the variance in BOLD signal. Event-related neural activity was modeled with delta (stick) functions representing face onsets convolved with the canonical hemodynamic response function and time derivative to provide a regressor for event-related BOLD-signal. Random effects analysis (Penny and Friston, 2003) was used for group statistics. A statistical threshold of P < 0.05 corrected for multiple spatial comparisons across the whole-brain was used, except for a priori hypothesized regions which were thresholded at P < 0.005 uncorrected (only clusters involving five or more contiguous voxels are reported). These a priori regions of interest included the temporal pole, FFG, STS, amygdalar, ventrolateral PFC, (vlPFC), ventromedial PFC (vmPFC), insula and ACC. Interactions between emotional context and faces were examined using t-tests. This approach is standard in imaging and has the advantage of specifying clearly the direction of interaction in every contrast (e.g. happy face being 'positively' modulated by happy context), which allows straightforward interpretations of the images.

RESULTS

Behavioral data

Our behavioral results replicated the main findings from previous behavioral studies using the 'Kuleshov Effect' (Carroll and Russell, 1996; Goldberg, 1951; Wallbott, 1988). Despite faces being identical across contexts, on average, both positive and negative contexts resulted in significantly different ratings of faces compared with those presented in neutral contexts and to subsequent post-scan 'out of context' ratings $(F_{1.4.18.2} = 17.68, P < 0.0005$: repeated-measure ANOVA: Greenhouse-Geisser corrected for non-sphericity; Figure 2a). Similarly, mental-state attribution for faces presented in positive and negative contexts significantly altered ratings compared with those presented in neutral context and post hoc ratings $(F_{1,2,16,1} = 7.07, P < 0.013;$ Figure 2b). Post hoc Fisher's LSD test confirmed a significant main effect when faces were juxtaposed with either positive and negative context compared with neutral context. Faces juxtaposed with neutral context and post-scan ratings of expression and mental-state were statistically indistinguishable ($\alpha = 05$). Moreover, the significant correlations between facial expression and mental-state ratings (Pearson's R = 0.884; P < 0.001one-tailed), neutral (R = -0.579; P < 0.03), negative contexts (R = 0.780; P < 0.001) and post-scan ratings (R=0.754; P<0.002) suggests a strong correspondence between the attributions of the actors' facial expression and mental-state.

We next conducted a 3×3 repeated measures ANOVA (3 face expressions \times 3 contextual categories) for behavioral responses in the scanner only. A main-effect was found for facial expression ($F_{2,26} = 21.3$, P < 0.001; corrected for non-sphericity) and context ($F_{1.1,26} = 22.5$, P < 0.001; corrected for non-sphericity). We also found a small, but significant interaction between face expression and context $(F_{4,76} = 3.2, P < 0.040)$, suggesting that each context had a different effect on each type of face (Figure 3a). We next examined the mental-state ratings associated with each type of facial expression (face expression × contextual category) which showed a main-effect found for context ($F_{1.1,26} = 24.4$, P < 0.0005: repeated-measure ANOVA; corrected for nonsphericity) and facial expression ($F_{2,26} = 18.4$, P < 0.0005). A marginally significant interaction between mental-state attributions and context was also observed ($F_{4.76} = 2.4$, P < 0.091) (Figure 3a, b).

fMRI data

Direct comparison between emotionally salient and non-emotionally salient context. We first examined how brain activity elicited by faces was altered by emotional contexts (negative and positive minus neutral). The expectation here was that salient emotional contexts would result in differential brain activity for otherwise similar faces (Ekman *et al.*, 1982). In keeping with this prediction,

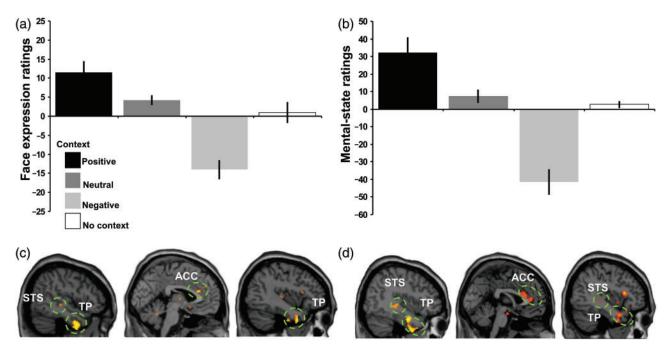


Fig. 2 (a) Mean percentage ratings and mean standard error (\pm s.e.m) ratings for face expression were significantly influenced by both positive and negative compared with neutral context and post-scan rating of faces. No significant differences were found between neutral faces and post-scan 'out of context' ratings. (b) Mental-state ratings showed a similar trend. Statistical parametric maps (from right hemisphere to left hemisphere) and parameter estimate plots illustrating the main effect of faces presented in the (c) negative-neutral contexts and (d) positive-neutral contexts. Faces presented in both negative and positive contexts resulted in increased activity in the STS (negative: 46, -40, -4; Z=2.88; positive: 56, -22, 2; Z=3.52), temporal pole (TP) (negative: 52, 2, -38; Z=4.17; positive: 42,4, -48; Z=3.62) and ACC (negative: -2, -28,

we observed that otherwise identical faces presented in the negative vs a neutral context (i.e. $N_{egative}C_{ontext} - N_{eutral}C_{ontext}$) led to enhanced activity in a priori regions of interest including the ACC, left STS, right STS, right amygdala and the bilateral temporal pole. A similar pattern was observed for the contrast of positive vs neutral contexts (i.e. $P_{ositive}C_{ontext} - N_{eutral}C_{ontext}$) with enhanced activation in the bilateral STS, bilateral temporal pole and the right ACC (Figures 2a,b and Table 1). These regions have been implicated in contextual processing of objects (Smith et al., 2004) and in the processing of socially relevant stimuli (Brothers, 1990).

Interaction between subtle emotional faces and emotional contexts. We further investigated effect of context on face processing by examining the interaction between emotional faces in congruent and incongruent contexts (Figure 3 and Table 2). We conducted four sets of analysis looking at the interaction between (i) fearful faces and negative $(N_{egative}C_{ontext}F_{ear}F_{ace} - N_{egative}C_{ontext}N_{eutral}F_{ace}) - (N_{eutral}$ $C_{ontext}F_{ear}F_{ace} - N_{eutral}C_{ontext}N_{eutral}F_{ace}$; (ii) happy between faces and positive context $(P_{ositive}C_{ontext}H_{appy}F_{ace} - P_{ositive}C_{ontext}N_{eutral}F_{ace}) - (N_{eutral}F_{ositive}C_{ontext}N_{eutral}F_{ositive})$ ContextHappyFace - NeutralContextNeutralFace); (iii) interaction between fearful faces and happy context

 $\begin{array}{l} (N_{eutral}C_{ontext}F_{ear}F_{ace}-N_{eutral}C_{ontext}N_{eutral}F_{ace})-(P_{ositive}\\ C_{ontext}F_{ear}F_{ace}-P_{ositive}C_{ontext}N_{eutral}F_{ace}) \ and \ (iv) \ interaction \\ between happy faces and fearful context \\ (N_{eutral}C_{ontext}H_{appy}F_{ace}-N_{eutral}C_{ontext}N_{eutral}F_{ace})-(N_{egative}\\ C_{ontext}H_{appy}F_{ace}-N_{egative}C_{ontext}N_{eutral}F_{ace}). \ We \ acknowledge \\ that \ this \ analysis \ is \ under \ power \ (i.e. \ only \ 12 \ events \ per \\ contrast), \ however, \ significant \ differences \ did \ emerge. \\ \end{array}$

The interaction between subtle fearful faces and negative context revealed activity in the right amygdala, fusiform gyrus and bilateral temporal pole and insula. Activity was also observed in the left hippocampus and vlPFC and vmPFC. The interaction between happy faces and the congruent positive context showed increased activity in the right amygdala, right temporal pole, right FFG, left hippocampus and bilateral insula. An interaction between fearful faces and the incongruent positive contexts was found in the right vmPFC and left insula. The interaction between happy faces and the incongruent negative context also elicited increased activity in the right vmPFC and bilateral amygdala.

Parametric modulation of BOLD signal by attribution ratings. We also estimated the effects of contextually driven attributions more directly by conducting a parametric analysis that examined the relationship between brain activity and subjective ratings of facial expression across

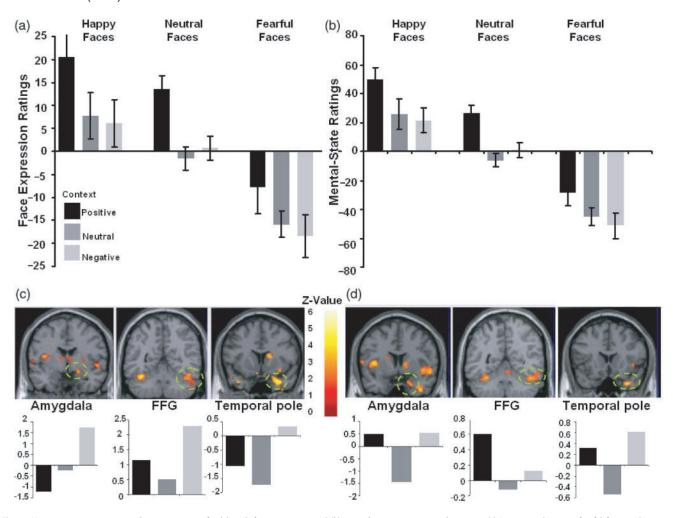


Fig. 3 Mean percentage ratings and \pm s.e.m ratings for (a) each face expression and (b) mental-state ratings in each context. (c) Interaction between fearful faces and negative context and betas for fearful faces presented in the positive (black bars), neutral (dark grey bars) and negative (light grey bars) contexts; (d) Interaction between happy faces and positive contexts and betas for happy faces presented in positive, neutral and negative contexts.

contexts for each category of face expression. Theoretically, because more ambiguous facial expressions produce the greatest contextual influence (Ekman et al., 1982), we were particularly interested in examining the neutral faces across contexts. The correlation between brain activity and positive attributions showed significant effects in the vmPFC, bilateral temporal pole and right anterior fusiform gyrus. The negative face expression attributions were associated with concomitant activity in the bilateral vIPFC, bilateral temporal pole and right FFG. These correlations were consistent with the hypothesis that the vmPFC and vlPFC mediate positive and negative attributions, respectively (Kim et al., 2004) (Figure 4a, b). Although not as significant, we also confirmed this ventral medial-lateral pattern by conducting the same parametric analysis with happy and fearful faces in respective contexts (Table 3). This dissociation was somewhat less consistent for the correlation with mental-state ratings. This finding is not surprising

given that mental-state attributions would presumably be less associated with valance increases.

DISCUSSION

Our environment conveys a rich array of contextual information which influences how the brain encodes, categorizes and recognizes objects and people (Bar, 2004; Smith et al., 2004; Cox et al., 2004). In relation to social cognition, context indicates appropriate behavior and influences how we perceive and appraise others (Gilbert and Malone, 1995; Ross, 1977). Using Kuleshov's paradigm, we provide behavioral evidence that when identical faces are juxtaposed with contextual movies of different valance, attributions of facial expression and mental-state are altered. fMRI data collected simultaneously revealed that, by contrasting faces juxtaposed with either positive or negative movies with those juxtaposed with the neutral movies, activity elicited by faces was altered in several

Table 1 Coordinates in MNI space and associated z-scores showing the BOLD differences for main effects of emotional minus neutral contexts

| Brain regions | Z-scores | Coordinates | | | |
|---|----------|-------------|------------|-----|--|
| | | X | γ | Z | |
| Main effect of negative context minus neutral context | | | | | |
| R amygdala | 2.64 | 34 | -2 | -18 | |
| R temporal pole* | 4.17 | 52 | 2 | -38 | |
| L temporal pole* | 4.49 | —40 | 6 | -40 | |
| L anterior cingulate cortex* | 3.03 | -2 | 28 | 20 | |
| L superior temporal sulcus* | 3.00 | -48 | -20 | 4 | |
| R superior temporal sulcus* | 2.88 | 46 | -30 | -4 | |
| L insula | 3.72 | -24 | 14 | -24 | |
| L insula | 3.73 | -50 | 24 | 6 | |
| Main effect of positive context minus neutral context | | | | | |
| R anterior cingulate cortex** | 3.74 | 8 | 50 | 12 | |
| R superior temporal sulcus | 3.52 | 56 | -22 | 2 | |
| L superior temporal sulcus* | 2.89 | -44 | -30 | 2 | |
| R temporal pole* | 3.26 | 42 | 4 | -48 | |
| L temporal pole* | 3.32 | —40 | 8 | -28 | |
| R insula | 2.83 | 38 | —12 | 8 | |
| L insula | 3.85 | -42 | 18 | 14 | |
| R amygdala | 2.54 | 22 | -2 | -26 | |

All values P < 0.005 uncorrected. *P < 0.05 small volume corrected. **P < 0.05 corrected for multiple comparisons.

Table 2 Coordinates in MNI space and associated z-scores showing the BOLD differences for the interaction between congruent and incongruent facial expressions and contexts

| Brain regions | Z-scores | Coordinates | | |
|--|----------|----------------|------------|-----|
| | | X | γ | Z |
| Interaction between fearful faces and negative context | | | | |
| R amygdala | 2.54 | 20 | -2 | -14 |
| R fusiform gyrus | 3.53 | 40 | -50 | -26 |
| R temporal pole | 2.81 | 34 | 12 | -32 |
| L temporal pole | 2.58 | -38 | 10 | -32 |
| L hippocampus | 3.60 | -28 | —18 | -12 |
| R vIPFC | 3.37 | 38 | 38 | -4 |
| R vmPFC | 3.19 | 24 | 54 | -4 |
| L insula | 2.95 | -62 | -8 | -2 |
| R insula | 3.28 | 66 | —12 | -4 |
| Interaction between happy faces and positive context | | | | |
| R amygdala | 2.44 | 22 | 8 | -28 |
| R temporal pole | 3.35 | 34 | 18 | -34 |
| R fusiform gyrus | 3.27 | 58 | -38 | -14 |
| L insula | 3.78 | -42 | 2 | 6 |
| R insula | 3.02 | 44 | 12 | -6 |
| L hippocampus | 3.27 | -24 | -22 | -12 |
| Interaction between fearful faces and happy context | | | | |
| L insula | 4.67 | -42 | 30 | 2 |
| R vmPFC/orbital frontal gyrus | 3.74 | 16 | 38 | -10 |
| Interaction between happy faces and fearful context | | | | |
| L amygdala | 3.99 | —14 | 2 | -18 |
| R amygdala | 2.43 | 18 | 2 | -28 |
| R vmPFC/orbital frontal gyrus | 2.33 | 4 | 48 | -10 |

All values P < 0.005 uncorrected.

regions of a priori interest including the bilateral temporal pole, STS insula and ACC. An interaction was observed in the right amygdala when subtle happy and fear faces were juxtaposed with positive and negative movies, respectively. An interaction between happy faces and negative context was also observed in bilateral amygdala suggesting that the amygdala may act to prime or tag affective value to faces. Parametric modulation of BOLD signal by attribution

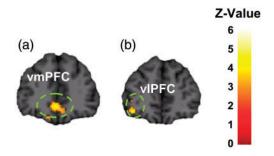


Fig. 4 Correlation between BOLD signal and (e) positive (vmPFC: 0, 44, -6, Z = 3.61) and (f) negative (vlPFC: -38, 46, -6, Z = 3.08) ratings of face expression associated with the neutral faces (Table 3).

ratings supported a role for the bilateral temporal pole for both positive and negative ratings and further illustrates a dissociation between vIPFC and vmPFC for negative and positive contextually evoked attributions, respectively.

Our results confirm the importance of contextual framing in social attributions. A multitude of social psychological studies support the hypothesis that contextual cues influence social attributions (Trope, 1986; Ross, 1977). Social attributions are likely to rely on activation of stored contextual schemata derived from experience (Levanthal and Scherer, 1987; Bar, 2004). Contextual frames may be integrated into social attributions through expectations where, based on experience, the attributor's judgments can be shifted from one category to another (Trope, 1986). Although the way affect is incorporated into attributions is likely to be a multiprocess (cf. Forgas, 1995), at the simplest level, these contextual shifts may occur via linear-weighted computations where the context and face are analyzed separately and the emotion perceived in the face is based on the weighted average from the two sources of emotion (Carroll and Russell, 1996). Therefore, the extent to which context shifts attributions may depend upon the source clarity of the stimulus (Ekman et al., 1982; Trope, 1986).

Table 3 Coordinates in MNI space and associated z-scores showing the BOLD differences correlations for face expression category and contexts

| Brain regions | Z-scores | Coordinates | Coordinates | | |
|------------------------------------|----------|-------------|-------------|------------|--|
| | | X | γ | Z | |
| Fearful faces—negative correlation | | | | | |
| R amygdala | 3.26 | 14 | 0 | -14 | |
| R fusiform gyrus* | 3.16 | 42 | —60 | -22 | |
| L fusiform gyrus** | 3.76 | —26 | -86 | -22 | |
| R temporal pole | 3.46 | 48 | 20 | -34 | |
| Fearful faces—positive correlation | | | | | |
| L temporal pole* | 3.93 | —46 | 2 | -40 | |
| R temporal pole* | 3.66 | 42 | 12 | -42 | |
| L vmPFC* | 3.30 | -6 | 54 | 10 | |
| R vIPFC | 3.16 | 34 | 40 | -14 | |
| Happy faces—negative correlation | | | | | |
| R vIPFC | 2.79 | 50 | 26 | -10 | |
| Happy faces—positive correlation | | | | | |
| R vmPFC | 2.66 | 2 | 46 | -10 | |
| R vIPFC | 3.16 | 32 | 46 | -14 | |
| R temporal pole | 3.22 | 44 | 4 | -34 | |
| L vIPFC | 2.60 | —34 | 42 | -10 | |
| Neutral faces—negative correlation | | | | | |
| L vIPFC | 3.08 | -38 | 46 | -10 | |
| R vIPFC | 2.87 | 28 | 52 | -8 | |
| L temporal pole | 2.82 | —40 | 8 | -42 | |
| R temporal pole | 3.04 | 46 | 4 | -42 | |
| R fusiform gyrus | 2.88 | 44 | -66 | -14 | |
| Neutral faces—positive correlation | | | | | |
| vmPFC* | 3.61 | 0 | 44 | -6 | |
| L temporal pole | 3.92 | —30 | 6 | -40 | |
| R temporal pole | 2.59 | 24 | 2 | -40 | |
| R frontal pole | 3.24 | 4 | 64 | 6 | |
| R fusiform gyrus | 3.01 | 40 | —42 | -20 | |

For example, in the present study, the subtle facial expressions are likely to be less salient than the highly valanced contextual movies. Contextual framing effects may be particularly evident when the context confirms, or is congruent with, expectations (Trope, 1996). Our behavioral results support such an effect showing that when congruent facial emotion and context are paired, subjects are most shifted in their attributions (cf. Ganis and Kutas, 2003; Davenport and Potter, 2004).

There is evidence that the temporal pole plays a key role in contextual framing (Smith et al., 2004). It has been theorized that the temporal pole serves as a repository for contextual frames or schemata (Ganis and Kutas, 2003; Smith et al., 2004; Cox et al., 2004). Acquired lesions in the vicinity of the right temporal pole can result in the loss of recognition of famous scenes, loss of memory for events and loss of person related knowledge (Tranel et al., 1997; Kitchener et al., 1999; Gorno-Tempini et al., 2004). In some cases, right temporal pole damage results in face processing deficits (i.e. prosopagnosia; Lough et al., 2006). This has led theorists to posit that the right temporal pole is part of an extended face system (Haxby et al., 2000; Calder and Young, 2005). Given the visual properties of this region, activity may also reflect the holding or recall of the contextual image in mind (Nakamura et al., 1994; Reiman et al., 1997; Lane et al., 1997). This theory seems unlikely given that examination of the null events did not reveal temporal pole activity (Table 4) and therefore supports a role for the temporal pole in face processing (Haxby et al., 2000; Calder and Young, 2005).

While the left temporal pole has been implicated in increased familiarity (Rotshtein *et al.*, 2005), possibly reflecting retrieval of semantic information about the person, this region could equally be involved in placing the person into the correct context (e.g. butcher on the bus phenomenon). Therefore, it might be expected that congruence would evoke more temporal pole activity than the incongruent conditions. This may happen because the congruent condition fits with previous experiences and expectancies. Further, the unexpectedness of the incongruent condition would presumably result in more cognitive effort

or search. This may account for the increased vmPFC when fearful and happy faces were presented in incongruent context. Taken together, our findings are consistent with previous suggestions that the temporal poles are involved in the storage and recall of contextual information, particularly when affectively salient (Smith *et al.*, 2004; Lane *et al.*, 1997). This proposal is anatomically plausible given that the temporal pole is well-connected to structures important in the processing of emotional and social information including the STS, amygdala and ventral PFC (Chabardes *et al.*, 2002; Kondo *et al.*, 2003).

The mechanism by which the temporal pole uses contextual information to modulate social attributions may depend upon the interaction with the STS with which it is strongly connected (Chabardes et al., 2002; Eifuku et al., 2004). The STS contains face-selective cells (Tsao et al., 2006) and has a particular role in the perception of changeable aspects of the face, such as emotional expression and eye direction (Haxby et al., 2000). Human imaging studies have implicated the STS in the explicit judgment of socially relevant information including trust, intentions, mental-state and diagnostic person information (den Ouden et al., 2005; Pelphrey et al., 2004; Winston et al., 2002; Mitchell et al., 2006) and may reflect more abstract aspects of mental-state attributions. One possibility is that activity in STS, a region of multisensory integration (King and Calvert, 2001), reflects the integration of contextual and facial cues. Alternatively, because STS activity was increased when faces were juxtaposed with positive and negative contexts, this region may be engaged when more detailed and explicit judgment of facial emotion is required (Narumoto et al., 2001). Such a theory is plausible given the strong connection between the STS and amygdala (Eifuku et al., 2004). Presumably, the emotional movie would drive expectation and attention towards a more explicit analysis of facial affect (Smith et al., 1996; Mitchell et al., 2006).

Intuitively, contextual framing relies on the integration of extrinsic contextual cues and the retrieval of stored knowledge about the likely emotional disposition of an actor in this context. Fitting with this theory, research

Table 4 Coordinates in MNI space and associated z-scores showing the BOLD differences for main effects of null events placed in emotional minus neutral contexts

| Brain regions | Z-scores | Coordinates | | |
|--|----------|-------------|-----|-----|
| | | X | Υ | Z |
| Null events in negative context minus null events in neutral context | | | | |
| R amygdala | 3.24 | 32 | 2 | -30 |
| R lateral extrastriate/fusiform gyrus | 3.72 | 46 | -56 | -10 |
| R vmPFC/orbitofrontal gyrus | 2.88 | 2 | 40 | -18 |
| Null events in positive context minus null events in neutral context | | | | |
| R vmPFC/orbitofrontal gyrus | 3.11 | 6 | 40 | -14 |

supports a role for the vPFC in top-down retrieval of information, particularly in relation to contextual guidance of social behavior (Bar, 2004). The vPFC has previously been associated with guessing and expectation, consistent with its role in top-down prediction (Frith and Dolan, 1997; Bar et al., 2006; Kao et al., 2005). The vPFC activity resulting from the parametric modulation of valance could be linked with top-down effects on a network of regions associated with contextually appropriate responses. The parametric increase in vPFC activity fits with its role in representing valance rather than intensity (Small et al., 2003; Anderson et al., 2003). This may occur in a Baysian fashion by constantly updating and integrating evidence about the present context with previously stored knowledge (Bar, 2004). Such an account is plausible given that both vIPFC and vmPFC project to discrete amygdala nuclei (Lissek and Gunturkun, 2005) and to other core and extended face processing regions including the STS, temporal pole and FFG (Dolan et al., 2001a; Haxby et al., 2000; Maratos et al., 2001). Whether directly or indirectly, the cytoarchitectonically distinct vlPFC and vmPFC may modulate the affective value of stimuli and act to guide choices across altering contexts (Kringelbach and Rolls 2004; O'Doherty et al., 2001; Kim et al., 2004). Such a theory fits with how affective states alter social judgments (Forgas, 1995), and studies showing that lesions to the vPFC can result in the inability to utilize previous experience to guide behavior (Damasio, 1994).

Greater activation in the vmPFC to null events for both positive and negative contexts (Table 4) may reflect insufficient information to direct behavior or a violation of expectation (Elliot et al., 2000). The vmPFC was also observed when faces were incongruent with the context, supporting fMRI data that this region is involved in the extent to which information is contextually appropriate (Kao et al., 2005). Moreover, ablation of primate vPFC suggests that this region is involved in integration of sensory signals which aid in choosing between competing responses (Izquierdo et al., 2005). Studies examining the effect of emotional context on objects (Smith et al., 2004) and words (Maratos et al., 2001) also suggest a role for the ACC in schema-based appraisals. In their study of context effects on surprised faces, Kim et al. (2004) showed the ACC to be functionally connected with both vmPFC and vlPFC when surprised faces were juxtaposed with positive and negative emotional verbal contexts, respectively. This suggests that these putative ACC (Smith et al., 1996) and vPFC appraisal systems interact. Together, our results suggest that the vPFC may act to guide appropriate responses across contexts. Other regions important in social cognition, including the dorsomedial PFC, may also be important in contextual framing and should be examined in future studies of context on socially relevant attributions.

Given the emotional nature of our faces and contextual movies, it is important to acknowledge the increased amygdala activity observed in this study. The amygdala has been implicated in the processing of socially relevant information (Brothers, 1990; Lieberman et al., 2005; Winston et al., 2002). In the current study, an interaction effect was observed in the right amygdala when subtle happy and fear faces were juxtaposed with positive and negative movies, respectively. An interaction between happy faces and negative context was observed in bilateral amygdala. Several mechanisms might account for this increased amygdala activity including affective priming (Dolan et al., 2001b), reinforcement history (Kim et al., 2004), intensity (Anderson et al., 2003) or tagging affective value to stimuli. Fitting with the latter hypothesis, amygdala damage impairs memory for gist, particularly in emotional contexts (Adolphs et al., 2005), and decreases perceptions of emotional salient events (Anderson and Phelps, 2001). A similar operation could take place during social attributions by facilitating attention towards an emotion expression (Bermpohl et al., 2006). Such an effect fits with our behavioral findings and studies of patients with focal amygdala lesions who show impairments in the recognition of facial emotions (Adolphs et al., 1999). Moreover, the amygdala is thought to influence visual areas including the FFG (Vuilleumier et al., 2004). This fits well with the increased FFG activity for the interaction between happy and positive context, and interaction between fearful faces and negative contexts. More broadly, our findings build on previous imaging studies demonstrating increased amygdala activity during the encoding and retrieval of neutral objects (Smith et al., 2004), surprised faces (Kim et al., 2004), and words (Maratos et al., 2001) juxtaposed with emotionally loaded contexts.

In summary, our results build on existing data showing contextual influences on behavioral and neurobiological systems underpinning socially relevant attributions. Our results suggest that a network of brain regions are involved in the storage and coordination of contextual framing. Although more research is needed, these regions may involve anterior temporal regions in the storage of contextual frames, the STS in the attention towards facial affects, and the amygdala in affective tagging of stimuli. Activity in these regions is likely to be influenced by top—down signals from the vPFC, which fits with its role in the contextual guidance of behavior. A better understanding of these complex systems will enable us to forge important links between affective neuroscience and social cognition.

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